A Review of the Genera *Crunomys* and *Archboldomys* (Rodentia: Muridae: Murinae), with Descriptions of Two New Species from the Philippines

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Abstract

The murine genera *Crunomys* and *Archboldomys* include species native to the oceanic Philippines and Sulawesi. Recent surveys in the Philippines have yielded additional specimens that help clarify generic definitions and species limits. These include examples of a new species of *Crunomys* from north-central Mindanao Island and a new *Archboldomys* from northeastern Luzon Island. Members of both genera are relatively small, ground-dwelling rodents that apparently are diurnal and insectivorous. There are important external, cranial, and chromosomal differences between the genera, and they share few derived traits that unite them as a group separate from other Philippine murids. Most of their morphological similarities may reflect either convergence or retention of primitive traits. *Archboldomys* is restricted to high-elevation forests on Luzon Island, whereas *Crunomys* is distinctive in having a broad distribution that includes much of the Philippines as well as Sulawesi. Most species of *Crunomys* occur at low elevations, and this may promote broader geographic distribution by facilitating dispersal across intermittent land bridges or by increasing the likelihood of rafting.

Introduction

A century ago, the genus *Crunomys* was described by Oldfield Thomas on the basis of a single specimen from northern Luzon Island (Thomas, 1898). When Guy Musser reviewed the genus *Crunomys* eight decades later, the number of specimens had increased only to seven; an additional specimen served as the basis for his description of the related Philippine genus *Archboldomys* (Musser, 1982). The "shrew-mice" of these genera are among the most elusive and intriguing members of the amazingly diverse murid fauna of the Philippine archipelago (Musser & Heaney, 1992; Heaney et al., 1997). Our recent field studies in the Philippines (Rickart et al., 1991; Heaney et al., 1997) have produced additional specimens of *Crunomys* and *Archboldomys* that serve as the basis for this report. These additional specimens help clarify generic definitions and species boundaries, and illuminate ecological traits and biogeographic patterns. Included among them are examples of two species new to the Philippine fauna, which we describe herein.

Specimens Examined and Methods

Specimens included in this study are deposited at the American Museum of Natural History, New York (AMNH); Natural History Museum, London (BMNH); Delaware Museum of Natural History, Greenville (DMNH); Field Museum of Natural History, Chicago (FMNH); Mindanao State University–Iligan Institute of Technology, Museum of Natural Sciences (MSU-IIT); Philippine National Museum, Manila (PNM); and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The following samples were examined: *Crunomys melanius*—CAMIGUIN: Camiguin Province, Mt. Timpoong, 2 km N, 6.5

km W Mahinog, 1275 m (FMNH 154861, 154862); Kital-is, Sagay Municipality, 6.5 km W Mahinog, 900–1100 m (MSU-IIT, two specimens); 0.5 km N, 6.5 km W Mahinog, 1000–1300 m (MSU-IIT, one specimen); LEYTE: Leyte Province, Mt. Lobi Range (DMNH 4222, holotype of *Crunomys rabori*); MINDANAO: Bukidnon Province, Mt. Katanglad Range, 17 km S, 7 km E Baungon, 1550 m (FMNH 147105, 147106); *Crunomys* n. sp.—holotype from MINDANAO: Bukidnon Province, Mt. Katanglad Range (see below); *Archboldomys luzonensis*—LUZON: Camarines Sur Province, Mt. Isarog (FMNH 95122, 147172, 147173; USNM 573834–573840); *Archboldomys* n. sp.—holotype and specimen in PNM from LUZON: Cagayan Province, Mt. Cetaceo, (see below).

Published descriptions of *Crunomys fallax* (Thomas, 1898; Musser, 1982) were augmented with information from recent photographs of the skin and skull of the holotype provided by P. Jenkins. Measurements and other information for specimens of *Crunomys celebensis* and additional specimens of *C. melanius* at AMNH and BMNH are from Musser (1982).

Measurements of total length (TOT), length of tail (LT), length of hind foot including claws (LHF), length of ear from notch (LE), and body mass (WT) were taken from original notes of collectors or from previous publications. Tail, hind foot, and ear lengths were measured directly for some specimens preserved in fluid. The length of head and body (LHB) was determined by subtracting length of tail from total length. The number of scale rings per centimeter (TSR) was counted at a point on the tail one-third the distance from the base, and the thickness of pelage was determined by measuring the total length of bunched hairs (LOF) in the mid-dorsal region.

The following cranial and dental measurements of adult specimens were made to the nearest 0.1 mm using dial calipers or a dissecting microscope and ocular micrometer, with limits as defined by Musser (1979, 1982): greatest length of skull (GLS), interorbital breadth (IB), zygomatic breadth (ZB), breadth of braincase (BBC), height of braincase (HBC), length of nasal bones (LN), length of rostrum (LR), breadth of rostrum (BR), breadth of zygomatic plate (BZP), breadth across incisor tips (BIT), length of diastema (LD), palatal length (PL), postpalatal length (PPL), length of incisive foramina (LIF), breadth of incisive foramina (BIF), distance from incisive foramina to M1 (IF-M1), length of palatal bridge (LPB), breadth of palatal bridge at M1 (PBM1), breadth of palatal bridge at M3 (PBM3), breadth of mesopterygoid fossa (BMF), length of auditory bulla (LB), height of auditory bulla (HB), alveolar length of maxillary molar row (LM1-3), crown length of M1 (LM1), crown breadth of M1 (BM1), length of mandible and incisor (LMI), length of mandible (LM), height of mandible (HM), length of mandibular toothrow (Lm1-3). Molar cusp terminology follows Musser and Heaney (1992).

For some specimens, karyotypes were prepared from bone marrow cells. Live-trapped animals were processed following the methods of Rickart et al. (1989). Freshly killed animals caught in snap traps were processed with a modified method involving in vitro incubation of cells in an isotonic colchicine solution followed by hypotonic treatment and fixation. Fixed cell suspensions were frozen in liquid nitrogen in the field, and standard karyotypes were prepared in the laboratory after storage at −70°C for several months. Chromosome terminology follows Rickart and Musser (1993).

Synopsis of Genera and Species

Crunomys Thomas, 1898

TYPE SPECIES—*Crunomys fallax* Thomas (1898: 394)

DIAGNOSIS—A genus of murine rodent distinguished by the following combination of characters: (1) small to moderate body size with a tail shorter than the combined length of head and body; (2) hind feet long and narrow with reduced first and fifth digits, and six plantar pads that are very small in relation to the entire plantar surface; (3) pelage short and thick, hair texture varying from soft to spiny; (4) patterned coloration, darkest on the muzzle, top of the head, mid-dorsally, on the rump, and on the dorsal surface of the legs, paler on the sides of the body, and much paler ventrally; (5) auditory bulla widely separated from the squamosal and alisphenoid by the enlarged and coalesced postglenoid vacuity and postalar fissure; (6) a pattern of cephalic arterial circulation characterized by the absence or extreme reduction of the stapedial foramen and artery and a secondary connection between the internal carotid and orbitomaxillary circulation; (7) loss or extreme reduction of cusp t3 on the first and second upper molars; (8) cusp t9 coalesced

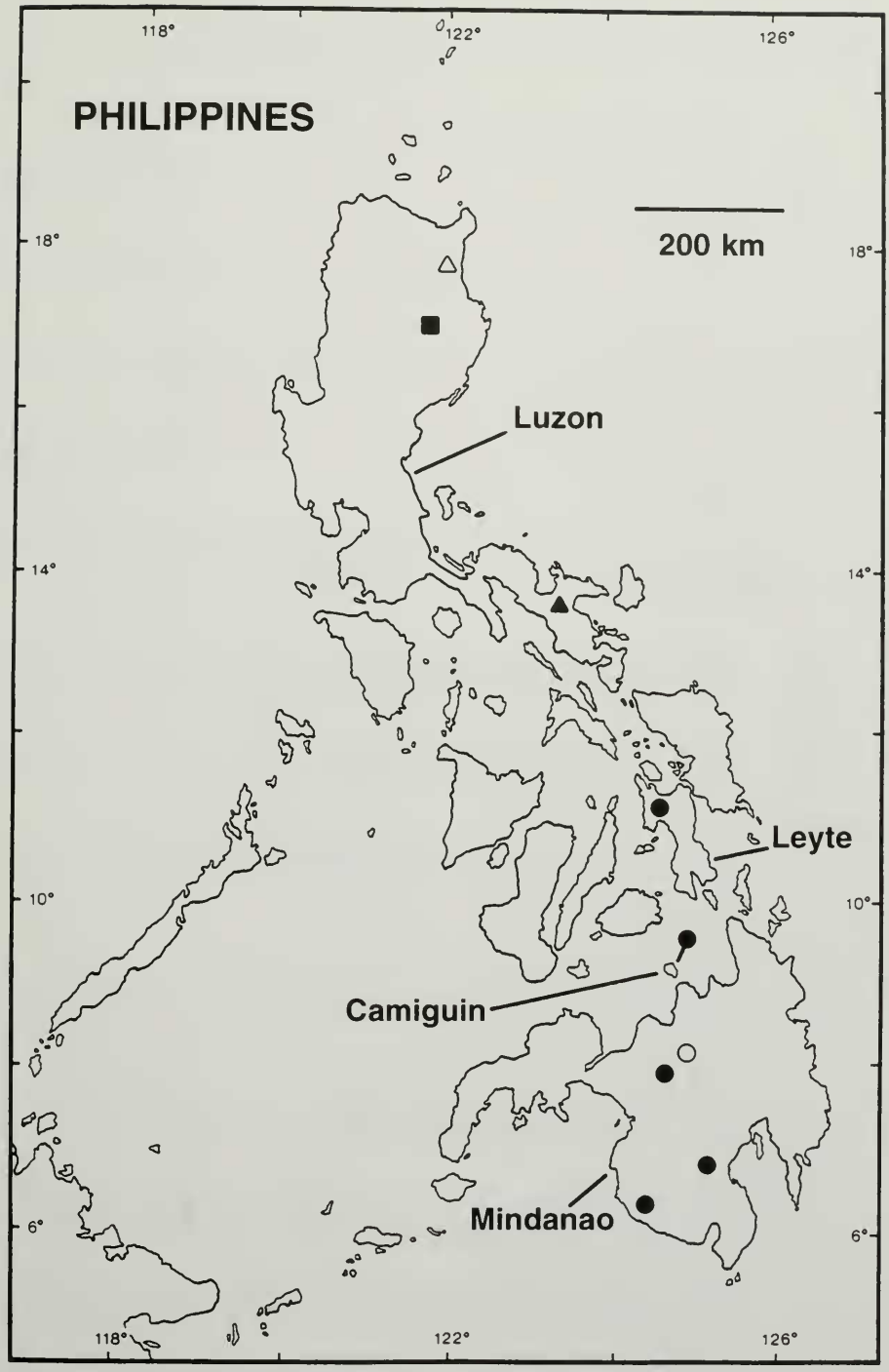

FIG. 1. Map of the Philippines with localities for *Crunomys fallax* (closed square), *C. melanius* (closed circles), *C. suncoides* (open circle), *Archboldomys luzonensis* (closed triangle), and *A. musseri* (open triangle).

TABLE 1. Measurements and other data from specimens of *Crunomys* and *Archboldomys*.

	Crunomys fallax[a]	*Crunomys celebensis*[a]			*Crunomys melanius*						*Crunomys suncoides*	*Archboldomys luzonensis*			*Archboldomys musseri*
	Luzon	Sulawesi			Mindanao				Camiguin	Leyte	Mindanao	Luzon			Luzon
	BMNH 97.4.8.4[b]	AMNH 224316[b]	AMNH 225042	AMNH 240490	BMNH 7.2.2.14[a,b]	AMNH 242102[a]	FMNH 147105	FMNH 147106	FMNH 154861	DMNH 4222[a,c]	FMNH 147942[b]	FMNH 95122[b]	FMNH 147172	FMNH 147173	FMNH 147176[b]
SEX	Male	Male	Female	Female	Male	Female	Male	Female	Male	Male	Male	Male	Male	Male	Male
AGE	Adult	Adult	Adult	Adult	Young Ad.	Adult	Adult	Adult	Adult	Adult	Adult	Adult	Adult	Adult	Adult
LHB	105	118	115	127	98	122	128	133	[136]	—	108	125	96	98	100
LT	79	82	80	84	68	79	[99]	95	94	90	101	70	66	72	88
LHF	23	25	26	27	25	26	29	27	29	27	27	28	28	28	24
LE	10	14	14	—	13	14	—	16	15	—	16	16	17	17	15
WT	—	55	55	35	—	—	71	58	—	—	37	—	—	—	—
LOF	4–5	5–6	5–6	5–6	4–6	5–6	4–6	4–6	5–6	5–6	5–6	9–11	8–10	9–11	7–8
TSR	—	20	19	20	18	18	15	16	16	14	20	16	15	15	24
GLS	—	29.0	—	30.2	28.2	30.0	31.6	31.3	33.0	32.1	30.7	28.2	27.4	26.8	26.6
IB	4.6	5.6	5.8	5.6	5.7	5.5	5.9	5.8	6.2	6.0	5.7	5.4	5.1	5.3	4.7
ZB	—	14.4	—	—	13.4	13.3	14.5	14.3	14.9	—	12.5	13.7	13.1	13.4	11.7
BBC	10.7	11.6	—	11.5	12.1	12.5	13.3	13.2	13.4	12.7	11.7	11.9	11.3	11.8	11.1
HBC	—	8.7	—	8.5	8.3	8.5	9.2	9.2	9.2	9.5	8.2	9.0	8.7	8.9	8.3
LN	9.3	12.1	12.6	13.0	9.8	11.2	11.9	11.7	13.0	13.1	11.7	10.1	9.8	9.6	10.3
LR	6.8	8.5	8.4	9.0	7.6	8.5	9.0	9.0	8.9	—	9.2	9.1	9.0	8.6	7.4
BR	4.3	5.9	5.9	—	5.4	5.1	5.8	5.4	6.1	5.6	5.1	5.2	5.3	5.3	4.5
BZP	1.5	2.2	1.8	1.9	1.5	1.8	2.0	1.7	1.8	2.0	1.5	2.1	1.8	1.8	1.3
BIT	1.4	2.3	2.2	—	1.5	1.7	1.9	1.7	1.9	1.8	1.5	—	—	—	1.5
LD	6.8	7.6	8.1	8.3	6.8	7.4	8.0	8.0	8.8	8.6	7.6	6.8	7.1	6.5	6.8
PL	12.7	13.2	14.2	14.4	12.7	12.9	14.6	14.1	14.7	14.6	13.1	12.9	12.7	12.7	12.6
PPL	—	11.7	11.5	—	10.8	12.0	13.0	12.8	13.5	13.3	10.4	9.9	9.8	9.3	10.2
LIF	3.6	4.1	4.4	—	3.8	4.1	4.5	4.7	4.4	4.5	4.3	4.4	4.3	4.2	3.2
BIF	1.6	2.0	2.0	—	2.1	2.1	2.5	2.3	2.7	2.3	1.9	2.0	2.0	2.1	1.8
IF-M1	—	1.4	1.3	1.4	—	1.4	1.2	1.1	2.5	1.6	1.5	0.5	0.8	0.7	1.2
LPB	4.9	5.6	5.6	5.1	5.1	5.1	5.6	5.2	6.5	5.7	5.6	5.3	5.6	5.3	5.6
PBM1	2.4	2.7	2.9	—	2.6	2.9	3.2	3.2	3.1	3.0	3.2	2.8	2.8	2.7	2.6
PBM3	2.7	3.0	3.1	—	3.2	3.3	3.4	3.5	3.8	3.4	3.5	3.3	3.5	3.3	3.2
BMF	1.8	1.8	2.1	—	1.6	2.2	2.8	2.6	3.0	2.7	2.5	2.1	2.4	2.2	1.9
LB	—	4.2	4.6	4.6	—	4.3	4.1	4.5	4.5	4.8	4.3	4.7	4.3	4.3	4.1

TABLE 1. *Continued*

	Crunomys fallax[a]	*Crunomys celebensis*[a]			*Crunomys melanius*						*Crunomys suncoides*	*Archboldomys luzonensis*			*Archboldomys musseri*
	Luzon	Sulawesi			Mindanao				Camiguin	Leyte	Mindanao	Luzon			Luzon
	BMNH 97.4.8.4[b]	AMNH 224316[b]	AMNH 225042	AMNH 240490	BMNH 7.2.2.14[a,b]	AMNH 242102[a]	FMNH 147105	FMNH 147106	FMNH 154861	DMNH 4222[a,c]	FMNH 147942[b]	FMNH 95122[b]	FMNH 147172	FMNH 147173	FMNH 147176[b]
HB	—	3.0	3.0	2.9	—	2.9	3.0	3.0	3.4	3.2	3.1	2.9	3.0	3.0	2.9
LM1-3	3.7	3.7	3.8	3.9	4.2	4.1	4.8	4.6	4.1	4.0	3.6	4.8	4.7	4.5	3.7
LM1	2.1	1.9	2.0	2.1	2.3	2.4	2.4	2.2	2.2	2.0	1.9	2.6	2.5	2.5	2.0
BM1	1.2	1.2	1.3	1.3	1.4	1.6	1.6	1.5	1.6	1.4	1.3	1.7	1.7	1.8	1.3
LMI	16.3	18.8	19.6	20.4	17.2	18.2	19.2	19.1	20.5	19.3	18.2	18.5	17.7	17.5	16.9
LM	12.4	15.5	16.6	17.0	13.9	16.2	16.4	16.2	16.9	16.5	16.3	15.6	15.2	15.3	14.5
HM	6.1	8.4	8.9	8.9	7.0	7.3	8.8	8.5	8.8	8.5	7.0	8.0	7.4	7.5	6.3
Lm1-3	3.8	3.8	3.9	4.0	4.3	4.2	4.6	4.3	4.1	4.1	3.8	5.1	5.1	5.2	4.0

[a] Measurements from Musser (1982).
[b] Holotypes.
[c] Holotype, *Crunomys rabori*.

with central cusp t8 on first upper molar and lost on second upper molar; (9) upper and lower third molars small relative to other molars and with a reduced number of cusps; (10) fusion of the anteroconid, metaconid, and protoconid of the first lower molar, together forming more than half of the occlusal surface (Musser, 1982; Musser & Heaney, 1992). *Crunomys* is most similar to the endemic Philippine genus *Archboldomys*. Detailed species comparisons are given by Musser (1982) and below under the descriptions of the new species.

Content and Distribution—As currently understood, the genus *Crunomys* contains four species distributed in the oceanic Philippines (Camiguin, Leyte, Luzon, and Mindanao islands) and in Central Sulawesi, Indonesia.

Crunomys fallax Thomas, 1898
Isabela shrew-mouse

Remarks—The genus *Crunomys* and the type species *C. fallax* were described from a single adult specimen collected in Isabela Province in northeastern Luzon (Fig. 1). The holotype remains the sole example of the species. It is a comparatively small murine rodent (Table 1), with a bicolored tail that is substantially shorter than the combined head and body length (Table 2). The pelage is harsh and spiny, grayish brown tinted with yellowish buff dorsally, darkest along the midline, paler at the sides, and pale gray ventrally. The specimen was shot during the day, along a stream at an elevation of 1000 ft (300 m) in "parched-up" (seasonally dry?) lowland forest (Thomas, 1898; Musser, 1982).

Crunomys celebensis Musser, 1982
Sulawesi shrew-mouse

Remarks—This species was described by Musser (1982) on the basis of three adult specimens collected in Sulawesi in 1974. It is the only member of the genus known to occur outside of the Philippines. *Crunomys celebensis* is larger than *C. fallax* and slightly smaller than adult *C. melanius* (Table 1). Color is similar to that of *C. melanius*; it is substantially darker than *C. fallax*, with less contrast between dorsal and ventral color and without a bicolored pattern on the tail. In contrast to both *C. fallax* and *C. melanius*, the pelage texture is soft rather than harsh or spiny. There are several distinctive cranial and dental features, including: prominent mastoid and maxillary fenestrae, a long and narrow palate, broad incisors, and relatively small molars (Tables 1, 2; Musser, 1982). The three specimens were trapped on or near the ground in streamside habitat, at mid-elevations between 2700 and 3500 ft. (820–1070 m) in lowland evergreen tropical rainforest. Two were captured at mid-morning, suggesting that the species is diurnal. Nothing is known of the food habits (Musser, 1982).

Crunomys melanius Thomas, 1907
Southern Philippine shrew-mouse

Synonym—*Crunomys rabori* Musser, 1982

Remarks—*Crunomys melanius* was described by Thomas (1907) on the basis of a single specimen collected on Mindanao Island in 1906. A second example, also from Mindanao, was obtained in 1923 (Fig. 1). Musser (1982) described *C. rabori* from one specimen collected on Leyte Island in 1964 (Fig. 1). This is an old adult male that is considerably larger and somewhat paler than the Mindanao specimens, both of which are younger. Musser and Heaney (1992) suggested that the morphological differences between these island samples might reflect age variation, and they questioned the distinctiveness of *C. rabori*. Our recent field surveys on Mindanao and Camiguin islands (Fig. 1) yielded seven specimens of *Crunomys* with external, cranial, and dental characteristics that agree with Musser's (1982) emended diagnosis of *C. melanius*. This series includes individuals of both sexes and various ages that span the gap in size and proportions seen between the earlier specimens from Mindanao and the one from Leyte (Tables 1, 2). They also display minor variation in color and texture of pelage. Two adults from Mindanao are dark brown above and grayish brown on sides and below and have harsh pelage with spiny dorsal awns. Four specimens from Camiguin are slightly darker overall with faint red or yellow tones; one adult has spiny dorsal awns, whereas a juvenile and two young adults have pelage that is stiff but slightly softer. Age appears to account for most of the variation in size and pelage characteristics in the total sample. Accordingly, we identify all of these specimens as *C. melanius*, and consider *C. rabori* to be a synonym.

Crunomys melanius has been collected in forested habitats from near sea level to 1550 m ele-

TABLE 2. Proportional relationships (percentages) for selected measurements of *Crunomys* and *Archboldomys*.

	LT/ LHB	ZB/ GLS	PPL/ PL	BR/ LR	LR/ GLS	LN/ GLS	BBC/ GLS	HBC/ BBC	LIF/ LD	LM1-3/ LPB	LM1-3/ GLS	Lm1-3/ LM	LB/ GLS	HM/ LM
Crunomys fallax														
BMNH 97.4.8.4	75	—	—	63	—	—	—	—	53	76	—	31	—	49
Crunomys melanius														
Mindanao														
BMNH 7.2.2.14	69	48	85	71	27	35	42	69	56	82	15	31	—	50
AMNH 242102	65	44	93	60	28	37	42	68	55	80	14	26	14	45
FMNH 147105	77	46	93	64	28	38	43	69	56	86	15	28	13	54
FMNH 147106	71	46	91	60	29	37	42	70	59	88	15	26	14	52
Camiguin														
FMNH 154861	69	45	92	69	27	39	41	69	50	63	12	24	14	52
Leyte														
DMNH 4222	—	—	91	—	—	41	40	75	52	70	13	25	15	52
Crunomys celebensis														
AMNH 240490	66	—	—	—	30	43	38	74	—	76	13	24	15	52
AMNH 225042	70	—	81	70	—	—	—	—	54	68	—	23	—	54
AMNH 224316	69	50	89	69	29	42	40	75	54	66	13	25	15	54
Crunomys suncoides														
FMNH 147942	94	41	79	55	30	38	38	73	57	64	12	23	14	43
Archboldomys luzonensis														
FMNH 95122	56	49	77	57	32	36	42	76	65	91	17	33	17	51
FMNH 147172	69	48	77	59	33	36	41	77	61	84	17	34	16	49
FMNH 147173	73	50	73	62	32	36	44	75	65	85	17	35	16	49
Archboldomys musseri														
FMNH 147176	88	44	81	61	28	39	42	75	47	66	14	28	15	43

vation. Two specimens from Mt. Katanglad, Mindanao, were trapped near holes on the ground in primary montane forest where some moss cover was present; the species appeared to be uncommon (Heaney et al., 1997). Five specimens from Camiguin were taken at elevations between 900 and 1275 m, in secondary lowland rainforest and in lightly disturbed and primary montane rainforest; the species apparently was at low densities at all sites, and it was trapped only beneath rotten logs and wood tangles in areas with few dead leaves and little moss (Heaney & Tabaranza, 1997).

During our survey of the Mt. Katanglad Range, we obtained another specimen of *Crunomys* that differs from previously known members of the genus. This represents a new species that we name and describe as follows:

Crunomys suncoides, new species (Figs. 2, 4–9)

HOLOTYPE—Adult male, FMNH 147942; collected 10 April 1993 (original number 5330 of L. R. Heaney); initially fixed in formalin, now preserved in ethyl alcohol with the skull removed and cleaned. The stomach and both femora have been removed; otherwise the specimen is in excellent condition. It is deposited at FMNH but will be transferred to PNM.

TYPE LOCALITY—Mt. Katanglad Range, 18.5 km S, 4 km E Camp Phillips, Bukidnon Province, Mindanao Island, Philippines, 2250 m elevation, 8°9′30″N, 124°51′E (Fig. 1).

DISTRIBUTION—Known only from the type locality in the Mt. Katanglad Range, but may occur elsewhere in high-elevation forest on the island of Mindanao.

REFERRED SPECIMENS—None. The holotype is the only known example.

MEASUREMENTS—Table 1.

ETYMOLOGY—The specific name *suncoides* refers to the striking superficial resemblance in body form to the common house shrew, *Suncus murinus*. We suggest the common name "Katanglad shrew-mouse."

DIAGNOSIS—A species of *Crunomys* grouped with other members of the genus and distinguished from *Archboldomys* by the following characters: (1) patterned pelage coloration, darkest mid-dorsally, paler on sides, and palest ventrally; (2) ventral maxillary roots of the zygomatic plates not overlapping the first molar; (3) absence of stapedial foramina and arteries, and a derived pattern of cephalic arterial circulation; (4) absence of squamoso-mastoid vacuities; (5) upper and lower third molars that are much smaller in comparison to the other molars. It is distinguished from other species of *Crunomys* and also from *Archboldomys* by the following combination of traits: (1) general orange brown pelage; (2) large front feet with long, stout claws; (3) sharply bicolored tail nearly equal in length to the combined head and body length; (4) narrow skull with a relatively long and narrow rostrum; (5) thin, elongate mandibles; (6) small molars, both absolutely and relative to the size of the skull and mandibles; (7) absence of cusp t9 from first upper molar; (8) presence of cusp t3 on second upper molar.

DESCRIPTION AND COMPARISONS—*Crunomys suncoides* is a small murine rodent (weight 37 g), with a narrow head, elongate snout, large feet with strong toes and claws, and a tail that is nearly as long as the combined length of head and body (Fig. 2). In most dimensions the new species is larger than *C. fallax* but smaller than other members of the genus (Table 1), and there are substantial proportional differences in external, cranial, and dental measurements (Table 2; Figs. 3, 4).

The new species has pelage that is dense and relatively short (Table 1), and soft as in *C. celebensis* rather than spiny or harsh as in *C. fallax* and *C. melanius*. Most hairs in the overfur are tricolored, uniformly pale gray for ¾ of the length from the base, followed by a narrow black band and an orange-brown tip. Ventral hairs are shorter and bicolored (gray with orange-brown tips).

The general pelage color is rich orange-brown, and it is patterned much as in other *Crunomys*. Color mid-dorsally, on top of the head and on the rump, is dark brown with slight orange tint, grading to a paler shade on the sides. Dorsal and lateral surfaces of the muzzle are blackish brown. Upperparts are slightly grizzled from a general scattering of uniformly pale gray hairs. Underparts are paler, but there is no sharp lateral delineation. The chest and upper belly are bright orange-brown, with more extensive gray on the throat and lower belly. The urogenital region is sparsely covered with short gray hairs, and the base of the tail behind the anus is blackish brown.

The snout is elongate, with a flexible cartilaginous tip 4 mm long. The rhinarium and lips are unpigmented. Each of the very small eyes (diameter ca. 2 mm) is surrounded by a narrow (ca. 1 mm) ring that lacks pigment or hair. Facial vi-

FIG. 2. Adult male *Crunomys suncoides* (FMNH 147942, holotype).

brissae are blackish gray and relatively short, the mystacials reaching no further than the ears. The pinnae are small, nearly naked, and nearly unpigmented. On the external surface of the pinna, there are only a few fine hairs near the base, with both density and diameter of hairs increasing slightly toward the margin. The internal surface is similar, but with even fewer, shorter, and finer hairs. Dorsal surfaces of the front and hind feet are unpigmented, sparsely covered with short silver hairs and with a scattering of slightly longer black hairs over the metapodials. The palmar surface is naked and unpigmented. The plantar surface is naked, with mottled pale gray pigmentation on the metapodials and unpigmented heel and digits.

In contrast to the other species of *Crunomys* and *Archboldomys*, the tail of *C. suncoides* is nearly as long as the head and body combined rather than substantially shorter (Table 2). The tail is sharply bicolored, as is the case with *C. fallax*, but unlike the other species. The dorsal surface and sides are uniformly dark grayish brown, and the undersurface is unpigmented. Scales are moderately small (20 rows per cm), and each is associated with three short (<1 mm), stiff hairs. Hairs on the dorsal surface are dark gray, whereas those on the underside are silver.

Compared to other *Crunomys*, the front feet are relatively large and have strong digits. There is a thick nail on the pollex, and the other digits have pale claws that are long, stout, and only slightly recurved. The palmar surface has five pads: three small interdigitals, a small medial metacarpal, and a large lateral metacarpal. The hind feet and digits are elongate and bear stout claws. The six plantar pads include four small interdigitals, a tiny medial metatarsal (hypothenar), and a larger lateral metatarsal (thenar); all are very small compared to the total plantar surface area.

The narrow, elongate head of *Crunomys suncoides* is reflected in the cranial structure. Viewed from above (Fig. 5), the skull is nearly triangular in outline. Compared to the other *Crunomys*, the rostrum is relatively long, narrow, and smoothly tapered (Table 2). The nasal bones are slender and have strongly sloping sides, giving the rostrum a tubular appearance. The frontal sinuses are inflated, and the interorbital region is relatively broad. The dorsolateral margins of the interorbital and

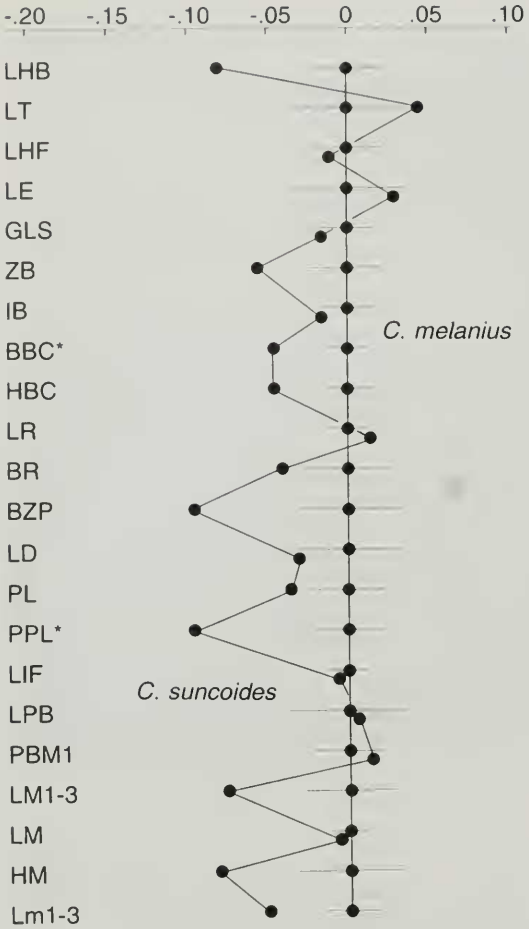

FIG. 3. Ratio diagram comparing log-transformed measurements of *Crunomys suncoides* to those of adult *C. melanius* (mean ± 2 standard errors [SE]). Asterisks denote measurements that differ significantly ($P < 0.05$; Student's *t*-tests).

postorbital regions and the braincase are entirely smooth, with no traces of supraorbital or temporal ridges. In comparison to the other species, zygomatic breadth and braincase breadth are modest relative to the overall length of the skull (Table 2; Figs. 3, 4). The zygomatic arches are thin and delicate, and are strongly backswept from their anterior roots. Zygomatic breadth exceeds braincase breadth only slightly. The braincase is narrow and rounded. The interparietal is relatively short (front to back) and narrow. The occiput is inflated posteriorly, projecting substantially beyond the occipital condyles.

Viewed laterally (Fig. 5), the dorsal profile of the skull of *C. suncoides* describes a nearly straight slope from the middle of the braincase to the nasal tips. The braincase is relatively flat dorsally, but it is inflated posteriorly to a degree not seen in other *Crunomys*. The tips of the nasal bones are straight and project slightly beyond the premaxillaries. Both the nasals and premaxillaries project beyond the anterior face of the incisors, forming a tubular nasal opening. The opening to the nasolacrimal canal at the base of the rostrum is conspicuous and directed dorsally, and the canal itself is moderately expanded. The relatively narrow zygomatic plate has a slightly concave anterior margin, and the posterior margin is even with the anterior edge of the first molar. In contrast to the other species of *Crunomys*, the zygomatic plate slants backward as in *Archboldomys luzonensis*.

There are features of the orbital region of *C. suncoides* that are distinctive. The orbit is constricted laterally by the slight outward bow of the zygomatic arch and medially by the extreme inflation of the frontal, maxillary, and palatine bones. In contrast to the other species of *Crunomys* and *Archboldomys*, the sphenopalatine foramen is nearly hidden at the anterior end of a deep, narrow groove formed by the near contact of the inflated orbital process of the palatine and the maxillary bone immediately above the molars. The position of the dorsal palatine foramen (which is coalesced with the sphenopalatine foramen in the other species) is obscured within this groove.

There is a structural difference between the left and right alisphenoid regions in the holotype. On the left side there is an alisphenoid strut forming the lateral wall of the alisphenoid canal and separating the foramen ovale accessorius from the coalesced masticatory and buccinator foramina. This same arrangement is characteristic of *Archboldomys luzonensis*. The right side lacks an alisphenoid strut and displays the general morphology seen in all other species of *Crunomys* (Musser, 1982, p. 35, fig. 23).

The squamosal, bullar, and mastoid regions of *C. suncoides* are similar to those of other members of the genus (Fig. 6A; Musser, 1982, p. 37, fig. 24). The bulla is broadly separated from the squamosal and much of the alisphenoid by the contiguous postglenoid vacuity and postalar fissure. The surface of the mastoid is slightly inflated and without fenestration. Along the dorsal margin there is a small mastoid foramen situated in the occipital suture. Along the anterior margin, the suture with the squamosal is entire and without the vacuity seen in *Archboldomys*. A squamoso-

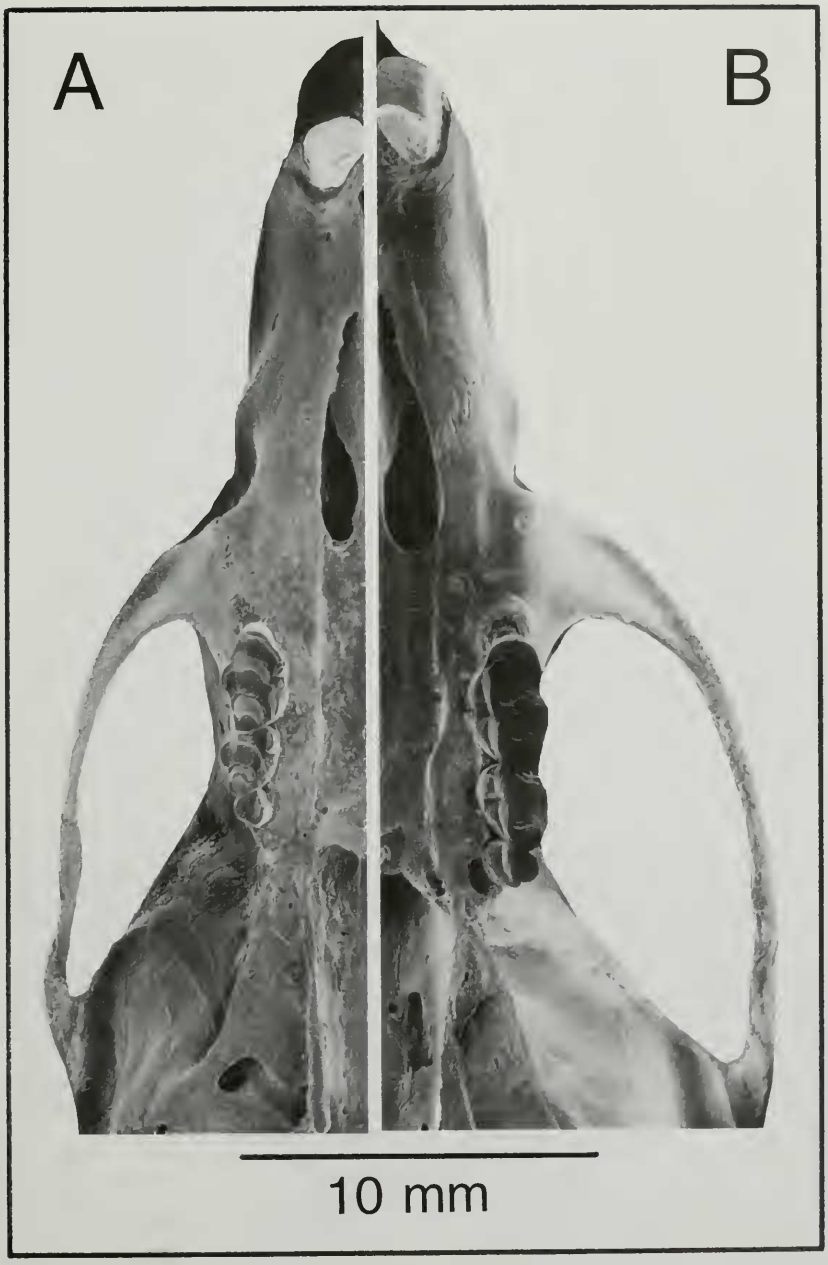

FIG. 4. Ventral views of the palatal region of **A**, *Crunomys suncoides* (FMNH 147942, holotype) and **B**, *Crunomys melanius* (FMNH 147105).

mastoid foramen cannot be located within the suture.

On the ventral aspect of the skull (Figs. 4A, 5) there is a small interpremaxillary foramen situated between the incisor alveoli. Each premaxilla has a prominent pit just posterior to the incisor. As in other species of *Crunomys*, the incisive foramina are narrow and short relative to the length of the diastema (Table 2). Lateral to the incisive foramina, the maxillae are fully ossified. The surface of the bony palate is slightly pitted, with prominent palatine grooves extending from the incisive foramina to the posterior border of the palatal bridge. The posterior palatine foramina are large,

FIG. 5. Dorsal, ventral, and lateral views of the cranium, and lateral view of the left mandible of *Crunomys suncoides* (FMNH 147942, holotype). Measurements are in Table 1.

but in ventral view they are partly hidden within the palatine grooves. They are located just anterior to the suture between the maxillary and palatine bones at a level opposite the posterior portion of the first molar. A pair of smaller foramina are located near the posterior border of the palate. The mesopterygoid fossa is narrow relative to the posterior breadth of the palate, and the sides and top are nearly complete, with sphenopalatine vacuities that are small in comparison to those of *C. melanius* or *A. luzonensis*.

As in other *Crunomys*, the surface of the pterygoid fossa is entire (Figs. 4, 7A), without the large sphenopterygoid vacuity seen in *A. luzonensis* (Musser, 1982, p. 44, fig. 30). On the posterior portion of the pterygoid plate, a short, diagonal

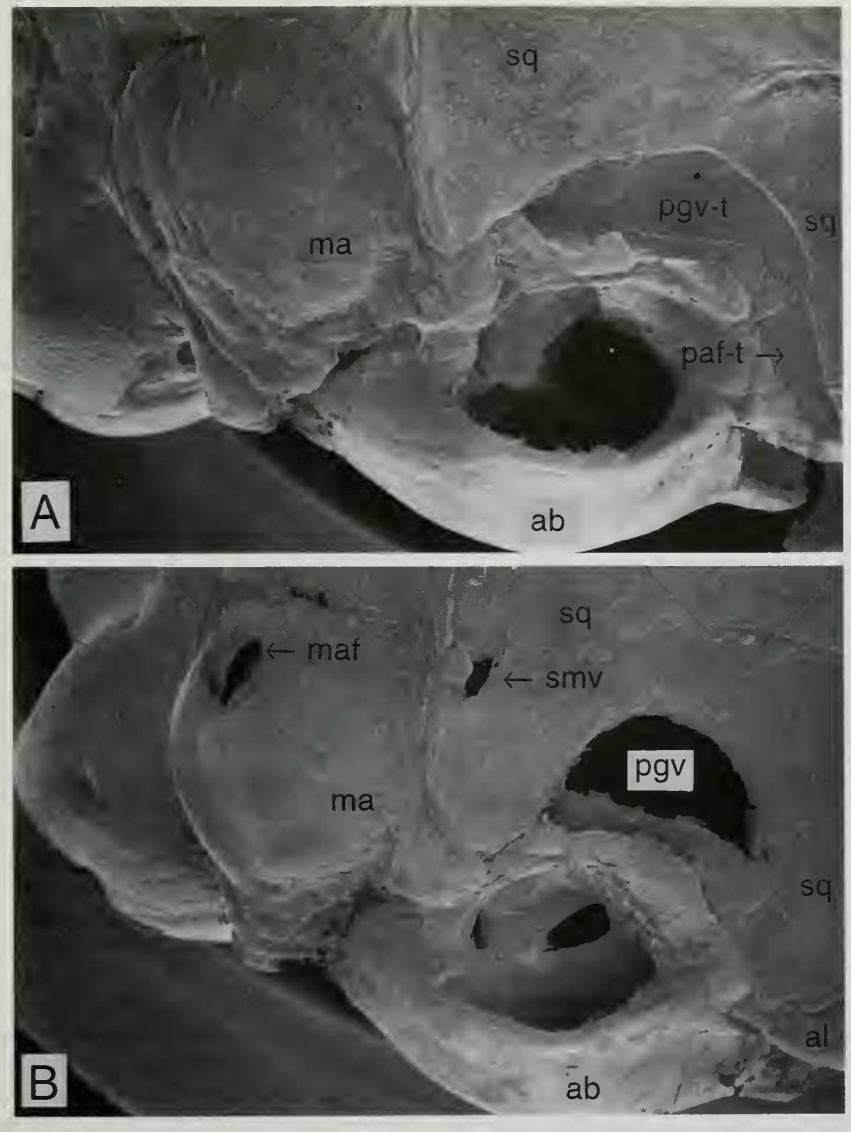

FIG. 6. Lateral views of squamosal, bullar, and mastoid regions of **A,** *Crunomys suncoides* (FMNH 147942, holotype) and **B,** *Archboldomys musseri* (FMNH 147176, holotype). Anterior is to the right. Abbreviations: ab, auditory bulla; al, alisphenoid; ma, mastoid; maf, mastoid fenestra; paf-t, postalar fissure covered by thin tissue; pgv, postglenoid vacuity; pgv-t, postglenoid vacuity covered by thin tissue; sq, squamosal; smv, squamoso-mastoid vacuity.

groove between the transverse canal and the posterior opening of the alisphenoid canal marks the path of a secondary branch of the internal carotid artery. This arrangement, presumed to be derived (Musser & Heaney, 1992), is seen in other *Crunomys*, but not in *Archboldomys* (Musser, 1982, pp. 44, 45, figs. 30, 31). As in *Crunomys melanius*, this arterial pattern is also reflected on the medial surface of each auditory bulla, where there is no trace of a stapedial foramen or artery (Musser, 1982, pp. 40, 41, figs. 27, 28).

In comparison to other species of *Crunomys* and *Archboldomys*, the mandibles of *C. suncoides* are exceptionally slender (Fig. 5; Tables 1, 2). The coronoid process is small in relation to the overall size of the mandible. The condyloid and angular processes are long and thin, resulting in a deeply concave posterior border. The labial surface of the mandible is relatively smooth. The bony ridge along the ventrolateral margin is less prominent than in *C. melanius*, extending from a point even with the middle of the first molar to the base of

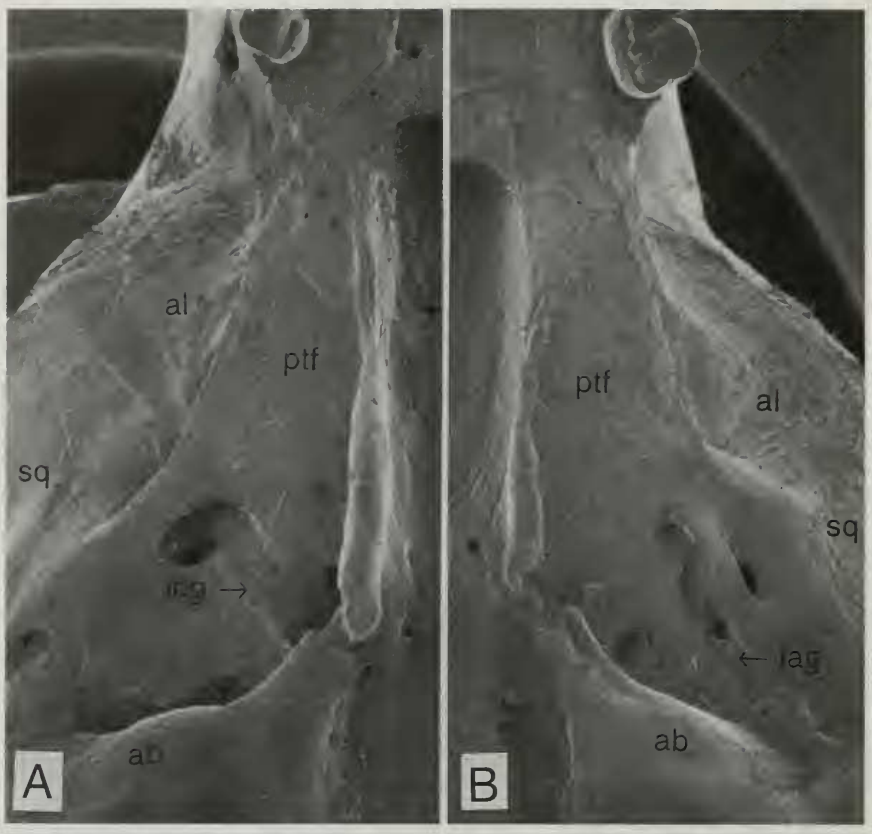

FIG. 7. Ventral views of pterygoid region of **A,** *Crunomys suncoides* (FMNH 147942, holotype) and **B,** *Archboldomys musseri* (FMNH 147176, holotype). Anterior is to the top. Abbreviations: ab, auditory bulla; al, alisphenoid; iag, groove for infraorbital branch of stapedial artery; icg, groove for secondary branch of internal carotid artery; ptf, pterygoid fossa; sq, squamosal.

the angular process. The base of the incisor capsule forms only a slight bulge below the coronoid. The shape and position of the mental and mandibular foramina are similar to those of the other species.

The enamel of both the upper and lower incisors is pale yellow. The upper incisors emerge at right angles to the rostrum and are slender, with a depth only slightly greater than the width. The delicate and elongate lower incisors describe a relatively shallow arc, and their anterior surfaces are rounded, causing the tips to wear to a sharp point. In contrast, *C. melanius* has upper incisors that are more than twice as deep as they are wide and strong lower incisors that curve more sharply, have flattened anterior surfaces, and have broader, chisel-shaped tips. The holotype of *C. suncoides* has molars that are extremely worn (Fig. 8A,C). The overall shape of the teeth and what remains of the cusp patterns resemble those of other *Crunomys* (Musser, 1982, pp. 13, 25, figs. 7, 15), although there are some distinctive features. In contrast to other *Crunomys*, the posterolabial cusp (t9) appears to be lost from the first upper molar. As in *C. fallax*, but in contrast to the other species of *Crunomys* and *Archboldomys*, a small anterolabial cusp (t3) is present on the second upper molar. Finally, the molars of *C. suncoides* are substantially smaller than those of all other *Crunomys* and *Archboldomys*, both absolutely and relative to the length of the palate and mandible (Figs. 4, 12; Tables 1, 2).

Although the holotype of *C. suncoides* was caught dead in a snap trap, it was very fresh when recovered, and it provided basic data on chromosomes. The standard karyotype (Fig. 9A) consists of 18 pairs of small- to large-sized chromosomes, all of which appear to be telocentric (2N = 36; fundamental number [FN] = 36). The sex chromosomes cannot be differentiated from the autosomes. No other species of *Crunomys* has been karyotyped to date. *Archboldomys luzonen-*

FIG. 8. Occlusal views of left molar toothrows of *Crunomys suncoides* (FMNH 147942, holotype; **A**, maxillary; **C**, mandibular), and *Archboldomys musseri* (FMNH 147176, holotype; **B**, maxillary; **D**, mandibular). Measurements are in Table 1. In *C. suncoides*, note the absence of cusp t9 from the first upper molar and presence of cusp t3 on the second upper molar. In *A. musseri*, note the presence of cusps t3 and t9 on the first upper molar.

sis has a diploid number of 26, a fundamental number of 43, and a distinctive sex chromosome system (Fig. 9B; Rickart & Musser, 1993, p. 8, fig. 5). These two karyotypes are quite different, although both have relatively low fundamental numbers near 40.

ECOLOGY—The holotype of *Crunomys suncoides* was taken in primary forest at an elevation 2250 m in the Mt. Katanglad Range. The type locality is located on a steep, north–south-oriented ridge on the northern flank of the range, with vegetation transitional between upper montane and lower mossy forest. Dominant trees include several species of gymnosperms and laurels. Forest canopy is 7–10 m high and broken by many tree falls. Breast-height trunk diameters of canopy trees are 8–30 cm. Emergent trees are 12–15 m high on the main ridge and 14–18 m on hillsides, with breast-height diameters of 40–100 cm. Epiphytes including moss, lichen, ferns, and orchids are common. Understory plants include saplings, *Rhododendron*, and other shrubs, ferns, and sedges. Substrate consists of rocky, volcanic soil covered with deep humus (10–50 cm) and thick surface leaf litter. The holotype was trapped near a small hole at the bottom of a small, steep gully on the west side of the main ridge just below the ridge crest. Other murids trapped at the type locality included *Apomys hylocetes*, *Apomys insignis*, *Batomys salomonseni*, *Limnomys sibuanus*, *Tarsomys apoensis*, and an undescribed species of *Limnomys*. The gymnure *Podogymnura truei* and the tree shrew *Urogale evereti* also were present. The shrew *Crocidura beatus* was trapped at adjacent lower and higher elevation sites, but it was not taken at the type locality. Bats recorded at the type locality included *Alionycteris paucidentata*, *Haplonycteris fischeri*, *Macroglossus minimus*, *Rhinolophus inops*, and *Pipistrellus javanicus*.

Long, slender hind feet with small plantar pads and a tail that is somewhat shorter than the combined head and body lengths indicate that *Cru-*

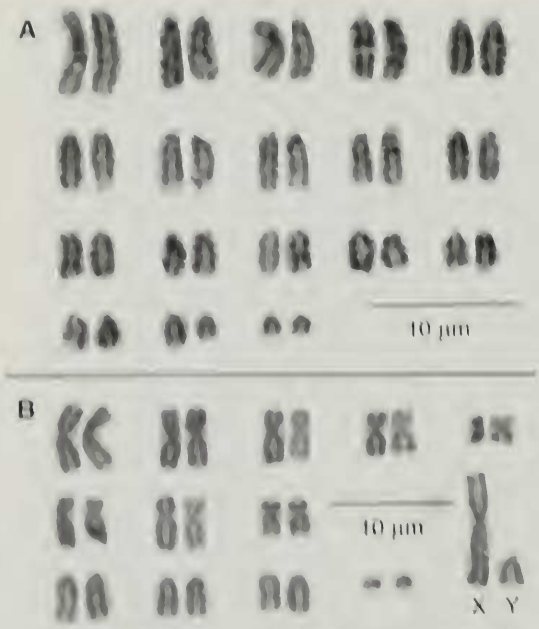

FIG. 9.—Karyotypes of **A**, *Crunomys suncoides* male (USNM 417942, holotype, 2N = 36) and **B**, *Archboldomys luzonensis* male (USNM 573505, 2N = 26, FN = 44). Sex chromosomes of *C. suncoides* cannot be distinguished from the autosomes.

nomys suncoides probably is terrestrial. Strong front feet with large claws, a narrow head, tiny eyes, and pelage that is soft and dense suggest a semi-fossorial habit. As is the case with other members of the genus, the species probably is diurnal. The holotype was captured mid-afternoon (ca. 1500 h) in a snap trap baited with a live earthworm. The small stomach was empty and there is no information on diet. The species may feed on soft-bodied invertebrates as does *Archboldomys luzonensis* (Rickart et al., 1991). The holotype is an old adult male that appeared to be in breeding condition when captured (firm, scrotal testes, the largest measuring 14 × 8 mm).

As is the case with other *Crunomys*, *C. suncoides* is difficult to capture; the single individual was obtained after more than 2,000 trap-nights at the type locality. It was not recorded at lower elevations on Mt. Katanglad despite more than 4,500 trap-nights between 1100 and 1900 m; however, its relative, *C. melanius*, was taken at 1550 m. Although *C. suncoides* was not detected above 2250 m, our trapping efforts at higher elevations were limited (732 trap-nights at 2375 m, 465 at 2600 m, and 310 at 2800 m).

The single high-elevation record for *Crunomys suncoides* is in sharp contrast to the known elevational distributions of its congeners. Elevation of the type locality exceeds the known upper elevation extremes for the other species of *Crunomys* by several hundred meters. *Crunomys suncoides* likely occurs in high-elevation forest habitat throughout the Mt. Katanglad Range, and it, or a near relative, may be present in areas of highland forest elsewhere on Mindanao.

The occurrence of two species of *Crunomys* in the Mt. Katanglad Range reflects a pattern seen among other murid genera from this region. The known localities for *Crunomys suncoides* and *C. melanius* are separated by 700 m elevation. The two species may have nonoverlapping elevational ranges, as is the case with *Tarsomys echinatus* and *Tarsomys apoensis*. In contrast, *Apomys insignis* and *Apomys hylocetes* have partially overlapping ranges on Mt. Katanglad, as do *Limnomys sibuanus* and an undescribed species of *Limnomys* (Musser & Heaney, 1992; Rickart & Heaney, unpubl. data).

Archboldomys Musser, 1982

TYPE SPECIES—*Archboldomys luzonensis* Musser (1982, p. 30).

DIAGNOSIS—A genus of small, terrestrial murine rodents that is most similar to *Crunomys*, but distinguished by the following characters: (1) long, soft fur without spiny or harsh awns; (2) overall dark, unpatterned pelage; (3) ventral maxillary root of the zygomatic plate partly overlapping first upper molar; (4) cephalic arterial circulation involving a prominent stapedial artery; (5) presence of an enlarged squamoso-mastoid vacuity; (6) slender mandible with elongate coronoid process; (7) molars with large, conical cusps; (8) upper and lower third molars larger relative to entire toothrow.

CONTENT AND DISTRIBUTION—As presently understood, the genus *Archboldomys* is confined to the Philippine island of Luzon and includes two species.

Archboldomys luzonensis Musser, 1982
Isarog shrew-mouse

REMARKS—The genus *Archboldomys*, with the type species *A. luzonensis*, was described by Musser (1982) from a single specimen collected on Mt. Isarog in southeastern Luzon. Subsequent sur-

FIG. 10. Adult male *Archboldomys musseri* (FMNH 147176, holotype). Scale bar = 5 cm.

veys of Mt. Isarog have yielded 13 additional examples of *A. luzonensis* that are consistent with Musser's original diagnosis. The species is known only from upper montane and mossy forest habitats above 1300 m elevation on Mt. Isarog. As is the case with *Crunomys*, *A. luzonensis* is difficult to capture: in one survey, only eight individuals were taken during 4,900 trap-nights (Rickart et al., 1991). Most of these were not attracted to baits but were caught because they ran across the treadles of snap traps positioned on the ground either in runways or directly in front of burrow openings. Stomach contents indicate a diet of invertebrates (adult and larval insects, terrestrial crustaceans, and earthworms). The species is probably strictly diurnal; most individuals were known to have been captured during daylight hours (Rickart et al., 1991).

Musser (1982) hypothesized that *A. luzonensis* or a close relative might occur in the high mountains of northern Luzon. This distributional pattern is seen among other endemic murid genera represented in the high-elevation fauna of Mt. Isarog (Musser & Freeman, 1981; Musser, 1982; Rickart & Heaney, 1991). Musser was correct. In 1992 a shrew-mouse was discovered in the northern Sierra Madre range of northeastern Luzon. The external and cranial features of this animal distinguish it as a second species of *Archboldomys* that we name and describe below.

***Archboldomys musseri*, new species**
(Figs. 6–10, 12, 13)

HOLOTYPE—Adult male, FMNH 147176; collected 15 May 1992 (original number 2092 of D. S. Balete); initially fixed in formalin, now preserved in ethyl alcohol with the skull removed and cleaned. The specimen is in excellent condition. Currently it is deposited at FMNH but will be transferred to PNM.

TYPE LOCALITY—Mt. Cetaceo, Sierra Madre Range, Callao Municipality, Cagayan Province, Luzon Island, Philippines, 1650 m elevation, 17°42′N, 122°02′E (Fig. 1).

DISTRIBUTION—Known only from the type locality but may be more widely distributed in the mountains of northern Luzon.

REFERRED SPECIMEN—One, from the same locality as the holotype, deposited at PNM.

MEASUREMENTS—Table 1.

ETYMOLOGY—Named in honor of Guy G. Musser, in recognition of his many outstanding contributions as the leading authority on Southeast Asian murid rodents. We suggest the common name "Sierra Madre shrew-mouse," in recognition of the newly declared Northern Sierra Madre Wilderness Park, the largest park in the Philippines.

DIAGNOSIS—A species of *Archboldomys* that is distinguished from all members of the genus *Cru-*

nomys and grouped with *A. luzonensis* by the following combination of characters: (1) overall dark, unpatterned pelage; (2) ventral maxillary roots of the zygomatic plates partly overlapping the first upper molar; (3) well-developed stapedial foramina and arteries, and retention of a primitive pattern of cephalic arterial circulation; (4) prominent squamoso-mastoid vacuities; (5) upper and lower third molars that are larger relative to the other molars. It is distinguished from *A. luzonensis* by: (1) smaller size; (2) longer tail; (3) narrower skull with a relatively shorter, narrower rostrum; (4) nasal bones with straight as opposed to upturned tips; (5) shorter incisive foramina; (6) absence of large sphenopterygoid vacuities; (7) relatively small postglenoid vacuities; (8) prominent mastoid fenestrae; (9) molars that are much smaller, both absolutely and proportionately; (10) presence of labial cusps t3 and t9 on the first upper molars.

Description and Comparisons—*Archboldomys musseri* is a small murid with a stocky body, small fore- and hind feet, and a tail that is slightly shorter than the combined length of head and body (Fig. 10). Its overall form is similar to that of *A. luzonensis*, but it is smaller (Table 1), and there are many proportional differences in external, cranial, and dental measurements (Table 2; Figs. 11, 12).

The new species has fur that is soft and long, as does *A. luzonensis*, but the mid-dorsal fur of *A. musseri* is somewhat shorter (Table 1). Dorsal hairs are tricolored; they are uniformly medium gray for about ¾ of the length from the base, followed by a black band with a reddish brown tip. Ventral hairs are shorter and have paler tips.

Coloration is very similar to *A. luzonensis*. The upperparts are uniformly dark reddish brown without the darker patterning on the head, legs, mid-dorsum, and rump characteristic of *Crunomys*. There is no sharp color delineation between the dorsum and venter, but the underparts are paler, with a yellowish gray cast. The lips have pale gray pigmentation, and the rhinarium is darker gray. The eyelids are edged in black and surrounded by a narrow (<1 mm) pale gray ring. Mystacial vibrissae are blackish gray and moderately long, extending beyond the ears. The small, round ears are uniformly dark gray with a sparse covering of dark hairs. Dorsal surfaces of the feet are uniformly pigmented (fore feet brownish gray, hind feet brownish black) and sparsely covered with short, dark hairs. Both the palmar and plantar surfaces are naked and pigmented dark brownish gray except for the pads, which are paler.

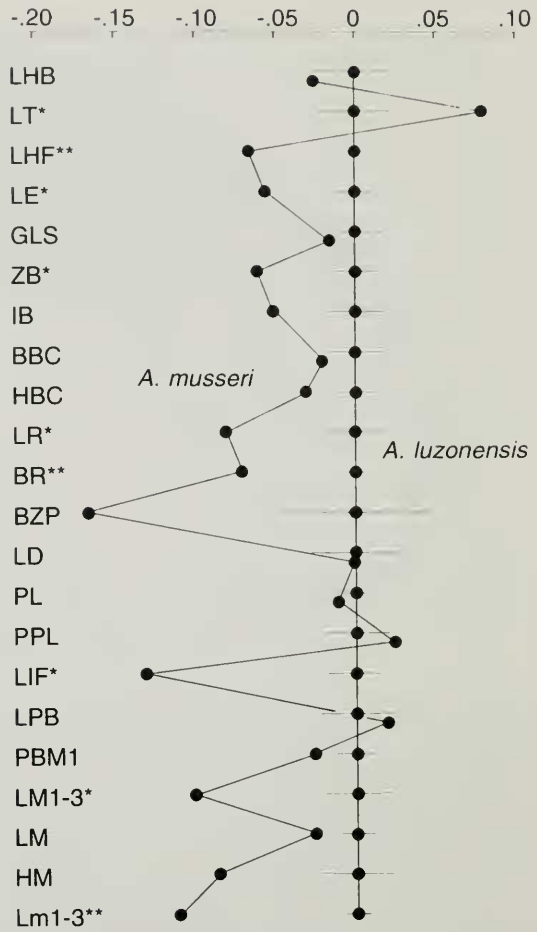

Fig. 11. Ratio diagram comparing log-transformed measurements of *Archboldomys musseri* to those of adult *A. luzonensis* (mean ± 2 SE). Asterisks denote measurements that differ significantly (* $P < 0.05$, ** $P < 0.01$; Student's *t*-tests).

The tail is shorter than the combined head and body length, but it is both relatively and absolutely longer than in *A. luzonensis* and is more finely scaled (Tables 1, 2; Fig. 11). The tail is uniformly blackish gray, without a bicolored pattern. There are three blackish hairs associated with each scale.

The front feet are relatively small, with slender digits. The hind feet and digits are long and narrow, but they are substantially smaller than in *A. luzonensis* (Table 1; Fig. 11). The pollex bears a nail, and all other digits have long, narrow claws that are nearly white in color. There are five pads on the palmar surface: three small interdigitals, a

FIG. 12. Ventral views of the palatal region of **A**, *Archboldomys musseri* (FMNH 147176, holotype) and **B**, *Archboldomys luzonensis* (FMNH 147173).

small medial metacarpal, and a larger lateral metacarpal. The plantar surface bears four interdigitals, a medial metatarsal, and a lateral metatarsal, all of which are relatively small.

The cranium of *Archboldomys musseri* is similar in general morphology to that of *A. luzonensis*, although it is substantially smaller in most dimensions (Table 1). Viewed dorsally (Fig. 13), the overall shape of the skull is elongate and narrow. Compared to *A. luzonensis*, the rostrum is short and narrow, and the nasals are elongate relative to the length of the skull (Fig. 11; Table 2). The interorbital region is relatively broad, and the surface of the postorbital area and the braincase are

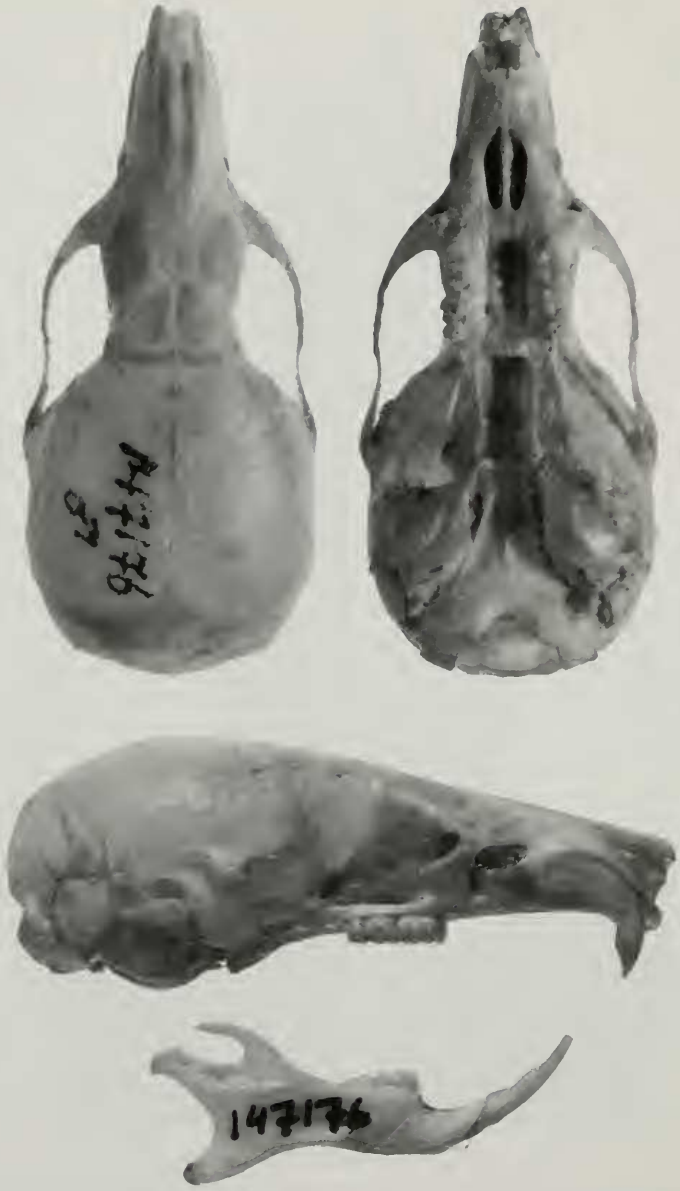

FIG. 13. Dorsal, ventral, and lateral views of the cranium, and lateral view of the right mandible of *Archboldomys musseri* (FMNH 147176, holotype). Measurements are in Table 1.

smooth and without ridges. Zygomatic breadth is modest relative to the length of the skull and the width of the braincase (Tables 1, 2), and the zygomatic arches are slender and delicate. The braincase is rectangular, as in *A. luzonensis*, but more elongate.

In side view (Fig. 13), the dorsal profile of the skull is nearly straight from the top of the braincase to the tips of the nasal bones. These are slightly damaged in the holotype, but they are clearly straight, rather than upturned, as in *A. luzonensis* (Musser, 1982, p. 21, fig. 13). The braincase is domed but not as inflated as in *A. luzonensis*. The nasal and premaxillary bones project only slightly beyond the anterior face of the incisors. The nasolacrimal canal slightly inflates the base of the rostrum. The opening of this canal is narrow and elongate, and it is directed slightly caudad. The zygomatic plate is narrower than in *A. luzonensis*, and the slightly concave anterior

edge is oriented vertically rather than slanting backward. However, in both species the posterior margin of the plate extends slightly behind the anterior margin of the first molar. The squamosal root of the zygomatic arch is positioned higher on the braincase than in *A. luzonensis*, substantially above the level of the postglenoid vacuity.

The sizes and positions of the orbital foramina in the new species are similar to those seen in *A. luzonensis*. The sphenopalatine foramen is closely associated with the dorsal palatine foramen, and together they form a long narrow opening in the ventral medial wall of the orbit.

On each side of the braincase there is a well-developed alisphenoid strut that forms the lateral wall of the alisphenoid canal and separates the foramen ovale accessorius from the coalesced masticatory and buccinator foramina. This is similar to the arrangement in *A. luzonensis* (Musser, 1982, p. 35, fig. 23), although the strut is considerably broader and more robust in the new species. The presence of an alisphenoid strut distinguishes the genus *Archboldomys* from all *Crunomys* with the exception of *C. suncoides* (see above).

The new species of *Archboldomys* exhibits a unique combination of features in the squamosal, bullar, and mastoid regions (Fig. 6B). The auditory bullae are similar in general structure to those of *A. luzonensis*, although they are less inflated. In clear contrast to *A. luzonensis* and all species of *Crunomys*, the postglenoid vacuity is relatively small and the postalar fissure not broadly open. As a result, the anterior margin of each bulla is in contact with the squamosal as well as the alisphenoid. As is the case with *A. luzonensis* (but unlike *Crunomys*), the squamoso-mastoid foramen is enlarged, forming a prominent vacuity along the posterior edge of the squamosal above each bulla. However, compared to *A. luzonensis* (Musser, 1982, p. 24, fig. 24), the vacuity is small, and that portion of the squamosal ventral to it is much broader. As in *A. luzonensis*, the occipital suture along the dorsal margin of each mastoid contains a small mastoid foramen. There also is a prominent mastoid fenestra near the dorsal margin of each mastoid. A comparable fenestra is seen in *Crunomys celebensis* (Musser, 1982, p. 38, fig. 25) but not in any of the other taxa.

In ventral view (Figs. 12A, 13), there are several distinctive cranial features. The prominent interpremaxillary foramen seen in *A. luzonensis* is absent, although there are several tiny paired foramina posterior to the incisors. The incisive foramina are short, both absolutely and relative to the length of the diastema, rather than long as in *A. luzonensis* (Tables 1, 2; Fig. 12). The maxillae lateral to the incisive foramina are fully ossified, and the surface of the bony palate is smooth. Shallow palatine grooves extend from the incisive foramina to the posterior palatine foramina.

The mesopterygoid and pterygoid regions of *A. musseri* include some distinctive features. The mesopterygoid fossa is narrow relative to the palate. Aside from a small, membrane-covered sphenopalatine vacuity on the right wall, the dorsal and lateral surfaces are entirely ossified. The surface of each pterygoid fossa is entire (Figs. 7B, 12A), without the sphenopterygoid vacuities seen in *A. luzonensis* (Fig. 12B; Musser, 1982, p. 44, fig. 30). The posterior portion of the pterygoid plate contains a groove for the interorbital branch of the stapedial artery (Fig. 7B). This constitutes the primitive arterial pattern seen also in *A. luzonensis*, and it is contrasted with the presumed derived pattern seen in *Crunomys* (Fig 7A; Musser, 1982, pp. 44, 45, figs. 30, 31). The pattern also is reflected in the large stapedial foramen and arterial channel on the medial surface of each auditory bulla; the same structures are present in *A. luzonensis* but are absent or very much reduced in *Crunomys* (Musser, 1982, pp. 40, 41, figs. 27, 28).

The mandibles of *A. musseri* (Fig. 13) are similar to those of *A. luzonensis* in general form and in the positioning of mental and mandibular foramina, but they are smaller and more slender (Tables 1, 2). The labial surface of the mandible is smooth, and there is no swelling at the end of the incisor capsule at the base of the coronoid process. A short ridge on the ventrolateral surface extends from the level of the second molar to the base of the angular process. The condyloid process is elongate and slender, and the condyle is relatively small. The angular process also is slender, so that the posterior margin of the mandible is deeply concave. Relative to the overall size of the mandible, the coronoid process is extremely long, thin, and backswept, extending back to a point even with the anterior edge of the condyle. To a lesser extent, *A. luzonensis* shares this trait, whereas all *Crunomys* have relatively short coronoid processes (Fig. 5; Musser, 1982, pp. 21, 91, figs. 13, 59; Musser & Heaney, 1992, p. 72, fig. 40).

The incisors of the new species are similar in general form to those of *A. luzonensis*, but they are more delicate. The slender upper incisors

emerge at right angles from the rostrum, and they have relatively flat anterior faces and straight-edged tips. The lower incisors are slender, with slightly flattened anterior surfaces and narrow, chisel-shaped tips. The enamel on the upper incisors is orange, and that on the lower incisors is a paler yellowish orange. Although the holotype of *A. musseri* has very worn molars (Fig. 8B,D), some important differences are evident in comparison to *A. luzonensis* (Musser & Heaney, 1992, pp. 70, 71, figs. 38, 39). The molars of the new species are much smaller, both absolutely and relative to palate and mandible lengths (Figs. 11, 12; Tables 1, 2). Small labial cusps t3 and t9 are present on the first upper molar of *A. musseri*, whereas these cusps are absent in *A. luzonensis*. In other respects, cusp patterns of the two species appear to be similar. In both species (but particularly *A. musseri*), the size of the upper and lower third molars relative to the other molars is much greater than in any *Crunomys*.

Ecology—Vegetation at the type locality was described by Danielsen et al. (1994) as "mossy forest . . . characterized by a low, dense and entangled forest with a canopy height decreasing with elevation from 10 to 3–4 m on the highest and more exposed parts. The canopy cover was 70–90 percent. The trees were densely covered by mosses and contained an abundance of epiphytes such as orchids, pitcher-plants (*Nepenthes*) and ferns." The specimens were initially misidentified as *Crunomys fallax*, and were reported as such by Danielsen et al. (1994). Other small mammals trapped in the area were *Apomys datae* and *Rattus everetti*; *Otopteropus cartilagonodus* and *Pipistrellus javanicus* were the only bats recorded despite an intensive netting effort.

The overall body form of *Archboldomys musseri* is similar in most respects to *A. luzonensis* and indicates ground-dwelling habits. However, the smaller, more delicate feet and digits and longer tail of the new species suggest a greater tendency toward above-ground as opposed to semifossorial activity.

Discussion

Phylogenetic Relationships

The discovery of new species and additional specimens of taxa that have been poorly represented allows us to reassess the definitions of *Crunomys* and *Archboldomys* and their relationships to other Philippine murids. Musser (1982) distinguished *Archboldomys* from *Crunomys* with a combination of external, cranial, and dental traits. These have changed somewhat as a result of this study. Some of the features in the original diagnosis of *Archboldomys* (elongate claws on the front feet, the presence of an alisphenoid strut, and slender mandibles) are no longer diagnostic because they are shared by *Crunomys suncoides*. Others (upturned nasal tips, elongate incisive foramina, long incisors, large sphenopterygoid vacuity, and absence of cusps t3 and t9 on the first upper molar) are not shared by *A. musseri* and therefore are diagnostic for *A. luzonensis* only. The remaining characters listed by Musser remain diagnostic, and they clearly define *Archboldomys* as a distinct genus. These are summarized as characters 1 through 8 in the brief generic account given above.

In describing *Crunomys celebensis*, Musser (1982) posed an alternative hypothesis that the morphological similarities between *Crunomys*-like mice of the Philippines and Sulawesi might represent convergence between independent groups. *Crunomys celebensis* differs from the Philippine *Crunomys* in many important respects, although all taxa share several characters that are presumed to be derived (Musser, 1982; this study). The discovery of *C. suncoides*, which shares some additional traits with *C. celebensis* (soft pelage, small molars, relatively narrow braincase), reduces the magnitude of difference. Other characteristics of the new species further expand the morphological range of the genus.

The principal obstacle in determining relationships of *Crunomys* and *Archboldomys* to other native Philippine murines is that both genera retain many primitive features (Musser, 1982; Musser & Heaney, 1992). They share the following derived morphological characters: (1) tail shorter than the head and body length, (2) elongate hind feet with small plantar pads, (3) reduction in size and number of molar cusps, (4) fusion of cusps on anterior half of first lower molar, and (5) reduced size and simplification of third upper and lower molars. These characters are shared also with the genera *Chrotomys*, *Celaenomys*, and *Rhynchomys*, and to a lesser extent *Apomys*, and they therefore serve to unite a sizable group of "old endemic" Philippine murids (Musser & Heaney, 1992). Whereas these other genera are characterized by additional unique specializations (Musser & Heaney, 1992), there are no clearly derived morphological traits

uniting *Crunomys* and *Archboldomys* as a distinctive group. There are similarities in shape, relative size, and general cusp patterns of molar teeth, but this may reflect dietary convergence.

Chromosomal data also support some broader relationships among old endemic Philippine genera. *Chrotomys* and *Rhynchomys* have very similar if not identical standard karyotypes (Rickart & Musser, 1993), supporting the hypothesis that these morphologically specialized shrew-rats are close relatives (Musser & Heaney, 1992). There has been considerable chromosomal evolution within *Apomys*, but features of some karyotypes support a broader grouping of this genus with *Chrotomys* and *Rhynchomys* (Rickart & Musser, 1993; Rickart, unpubl. data), as hypothesized by Musser and Heaney (1992).

Our results demonstrate substantial chromosomal differences between *Crunomys suncoides* and *Archboldomys luzonensis*. Both taxa have low fundamental numbers, but they are otherwise dissimilar and differ from other Philippine murines, which have fundamental numbers of 50 and above (Rickart & Musser, 1993). Among Indo-Australian murine rodents that have been karyotyped, very few exhibit fundamental numbers below 45 (Rickart & Musser, 1993, p. 22, fig. 8). *Crunomys suncoides* resembles species of *Cremnomys* from peninsular India (2N = 36; FN = 36–37; Gadi & Sharma, 1983) in possessing a complement of 36 telocentric elements. However, this similarity is probably coincidental because there are no obvious morphological features linking *Crunomys* with the long-tailed, scansorial *Cremnomys*. To date, there have been no cladistic analyses of relationships based on morphology, karyology, biochemical genetics, etc.; such studies are clearly needed.

Biogeography and Ecology

Crunomys is unique in being the only murid genus endemic to both Sulawesi and the Philippines (Musser, 1982). Most of the species have very limited known ranges, but this may be an artifact of their scarcity in collections. Despite the fact that it is represented by only 10 specimens, *Crunomys melanius* has an exceptionally broad range. In addition to a relatively wide distribution on Mindanao, it is also represented on the Mindanao land-bridge island of Leyte, as well as the more isolated (but nearby) oceanic island of Camiguin (Fig. 1). Among the 15 murid species on Mindanao, only *Crunomys melanius* and *Rattus everetti* occur on more than one Pleistocene island (Musser & Heaney, 1992; Heaney et al., 1997).

The unusually broad range of *Crunomys melanius* may reflect a general relationship between geographic and elevational distributions within Philippine murids. Most species are restricted to mid- or high-elevation montane and mossy forest habitats and are limited geographically to no more than one of the Pleistocene land-bridge island groups (Heaney, 1986; Heaney & Rickart, 1990). This is true for both species of *Archboldomys* as well. In contrast, *Crunomys* principally occurs in low-elevation habitat. Nearly all specimens of *Crunomys* have been found in lowland dipterocarp and lower montane forest habitats below 1500 m elevation; *C. suncoides* is the only species known to occur at higher elevations. Broad geographic range is apparent in a few other Philippine murids that occur at low elevations. *Rattus everetti* has a very broad elevational range that includes lowland dipterocarp forest, and it is the most widely distributed native rodent in the oceanic Philippines, occurring on most of the major island groups (Heaney & Rickart, 1990; Heaney et al., 1997). *Chrotomys mindorensis* is a low-elevation species found on two Pleistocene islands, Mindoro and Luzon (Rickart & Heaney, 1991). Occurrence at low elevations may promote broader geographic distribution in these taxa by facilitating dispersal across land-bridge islands during periods of lower sea level (Heaney, 1986) or by increasing the likelihood of over-water rafting to more isolated islands (perhaps during the frequent regional typhoons).

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